

DISPERSAL BY MALE DORYLINE ANTS IN WEST AFRICA*

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INTRODUCTION

Sausage-flies, the giant males of Old World doryline ants, are among the more conspicuous forms of tropical insect life, never failing to intrigue the observer by their numbers, size and bumbling flight. If we follow the conventional classification and include the New World Ecitonini within Dorylinae (*cf* Brown, 1973; Gotwald, 1977) there is a large literature—on the group's systematics, biogeography, and behaviour—but little of it quantitative.

At Legon, Ghana, 5°40' N, a 125 watt ultraviolet light-trap was run, the aim primarily to extend an investigation of seasonality in insects commenced earlier at Tafo, a little to the north (Gibbs and Leston, 1970). However, the facts collected on doryline flights fill a gap in our knowledge and can be viewed in several ecological contexts.

Legon was once forested and lies within the 'southern marginal' forest category of the scheme of Hall and Swaine (1976). It is today an area of derived savanna interspersed with gardens and small plots of food crops but some secondary forest survives about six miles distant. Climatological data for Accra, taken for over 30 years three miles south of Legon, are given in the form of a Leston-Gibbs climograph (Fig. 1) (Leston and Gibbs, 1971).

The original data and summary sheets are deposited, together with examples of the species collected, in the British Museum (Nat. Hist.), London.

Sudden heavy rain led to the breakdown of the trap on a few occasions: the missing samples were corrected for by dividing the numbers trapped in each 20-day period by the actual total of sampling days and adding this mean (or a multiple of it) to the total. The

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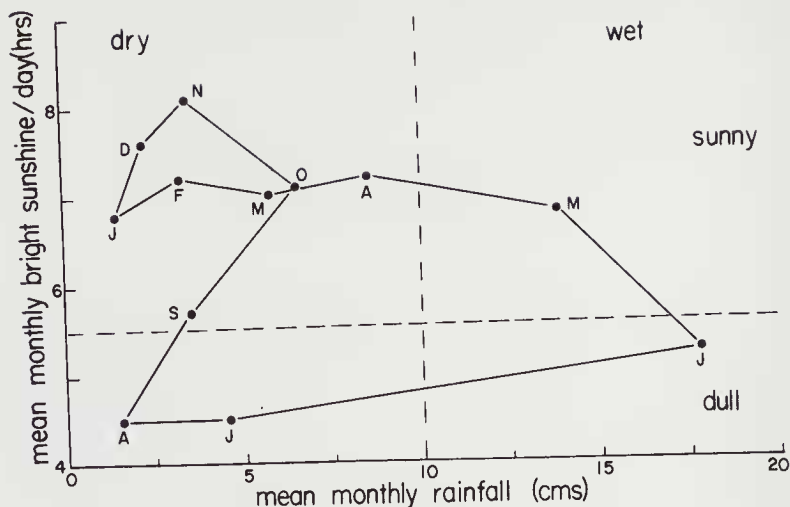


Fig. 1 Leston-Gibbs climograph for Accra, Ghana.

overall results, however, would have been the same even uncorrected.

The insects of this study are Dorylini. Aenictini were also sampled for a while but identification of the eight or nine species, distinguishable only by the male genital structures, was too complex and their study was abandoned.

RESULTS

The trap was run for 400 days (1730 hrs to 0600 hrs). The Dorylini collected are listed together with the corrected number of each:

1. <i>Alaopone atriceps</i> (Shuckard)	2470
2. <i>Typhlopone fulvus</i> Westwood	653
3. <i>Dorylus</i> sp 15	410
4. <i>Rhogmus fimbriatus</i> Shuckard	115
5. <i>Anomma nigricans</i> (Illiger)	88
6. <i>Dorylus</i> sp 14	7
7. <i>Dorylus</i> sp 16	4
8. <i>Dorylus</i> sp 19	3
9. <i>Rhogmus</i> sp 17	2
10. <i>Dorylus</i> sp 6	1
11. <i>Alaopone</i> sp 18	1
Total	3754

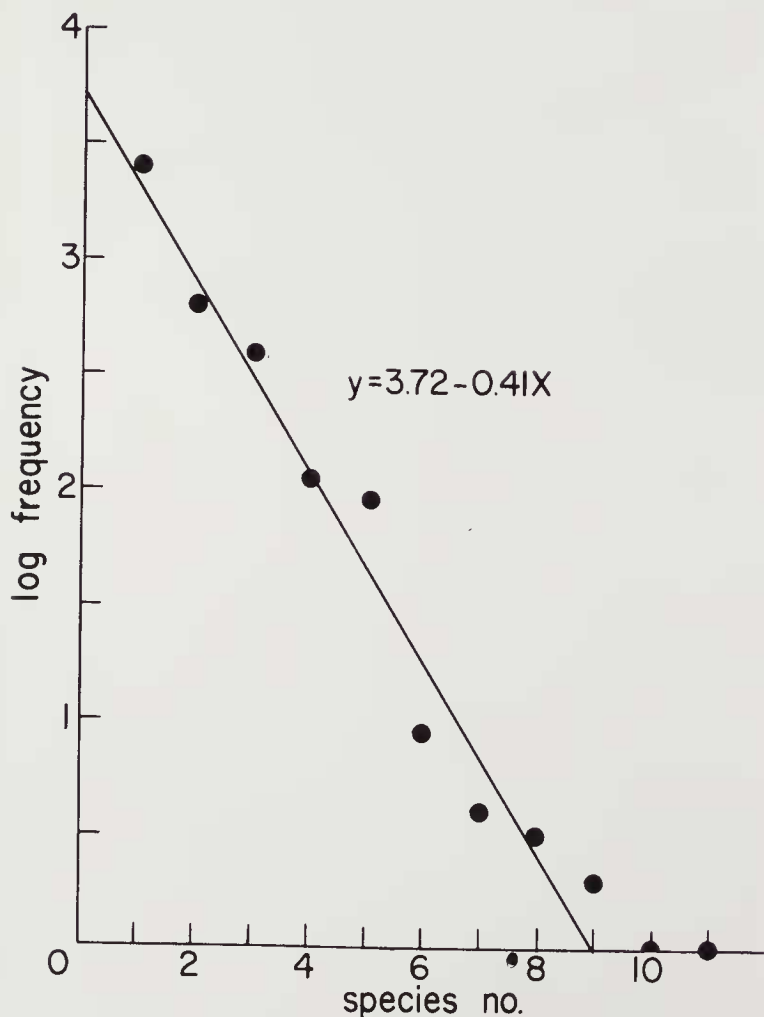


Fig. 2. Log frequencies (y) of the trapped species, species identification number (x) and the regression of y on x .

The number trapped of species 1 through 11 were transformed to logarithms and the regression coefficients calculated for y (frequency) on x (the species' number). (Fig. 2). There is a highly significant agreement with a log distribution hypothesis ($\chi^2 = 0.32$, $DF = 7$, $p > 0.99$).

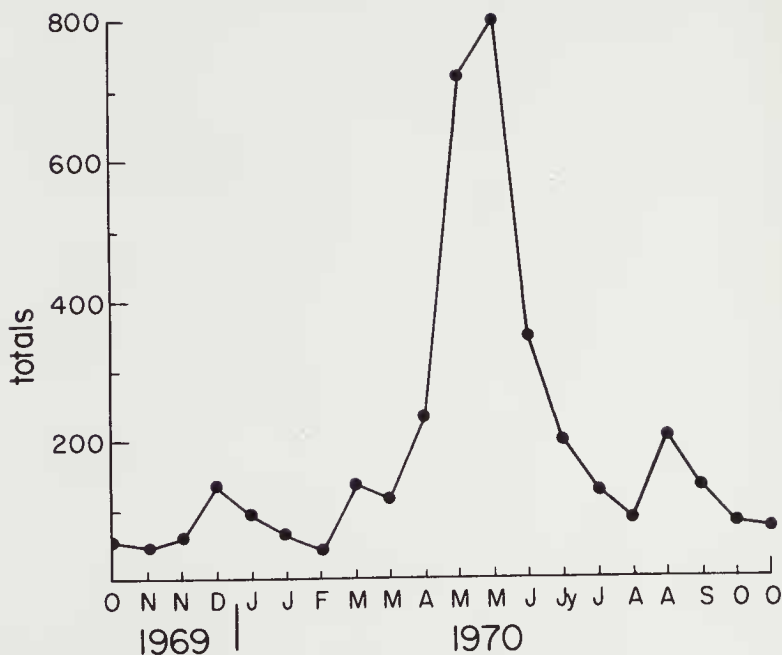


Fig. 3. Totals of male Dorylini trapped by an ultraviolet light trap at Legon, near Accra, grouped in 20-day classes.

The periodicity of the total sausage-flies captured, corrected and grouped in 20-day classes, is shown in Fig. 3. The five most abundant species accounted for over 99.5 percent of the entire catch and the leading four (97.18 percent), when their numbers are plotted (Fig. 4), show markedly similar periodicities. Kendall's index of concordance, W , was calculated, correcting for tied values:

$$n \text{ (number of sampling classes)} = 20$$

$$k \text{ (number of species)} = 4$$

$$W_2 = 0.51$$

$$\chi^2 = 38.76$$

$$DF = 19$$

$$0.01 > p > 0.001$$

The value of p confirms that the similarities could scarcely be due to chance. The fifth species, *Anomima nigricans*, was producing males, as were the first four, more or less throughout the year. However, its peak numbers occurred in mid-September through early October (Fig. 5), and not March to May as in the first four.

Besides the major annual period of abundance the species showed rhythmic pulsations in frequency. In April through June the periodicity was around 29 to 32 days, in December through February around a day or two less. The periodicities were clear cut in *Alaopone atriceps* and *Typhlopone fulvus* (Fig. 6), less obvious—because of the lower numbers taken—in *Dorylus* sp 15 and *Rhogmus fimbriatus*.

The trapped material was assessed in terms of the i^{th} species (Fig. 7). The first ten were amassed rapidly and were present by day 56, in the third sampling period (Fig. 4). However, the eleventh species

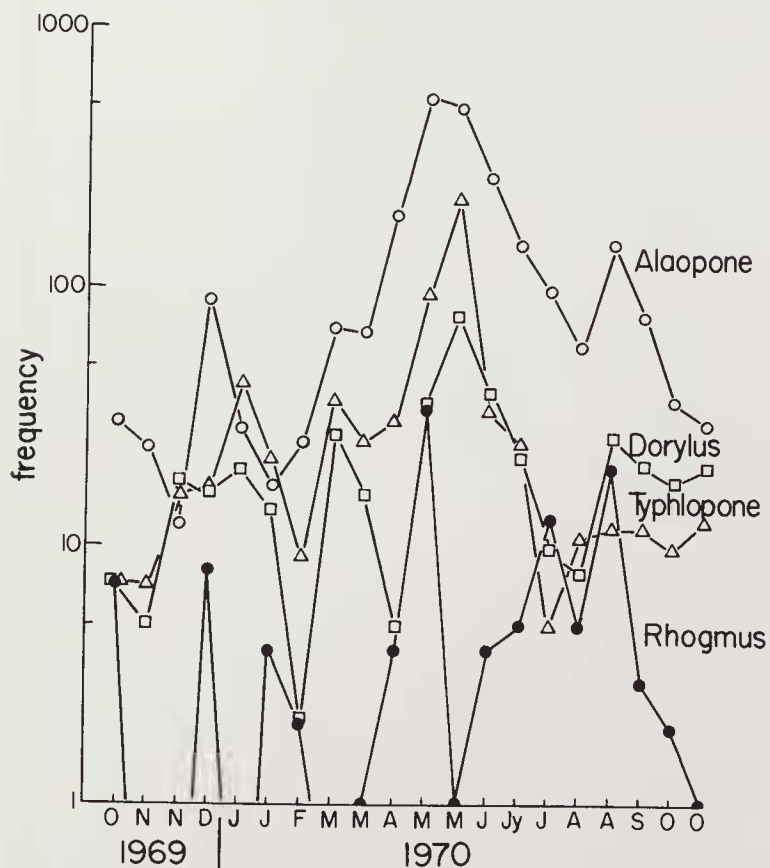


Fig. 4. Totals of the four most abundant species in the Legon samples, logarithmic, grouped in 20-day classes.

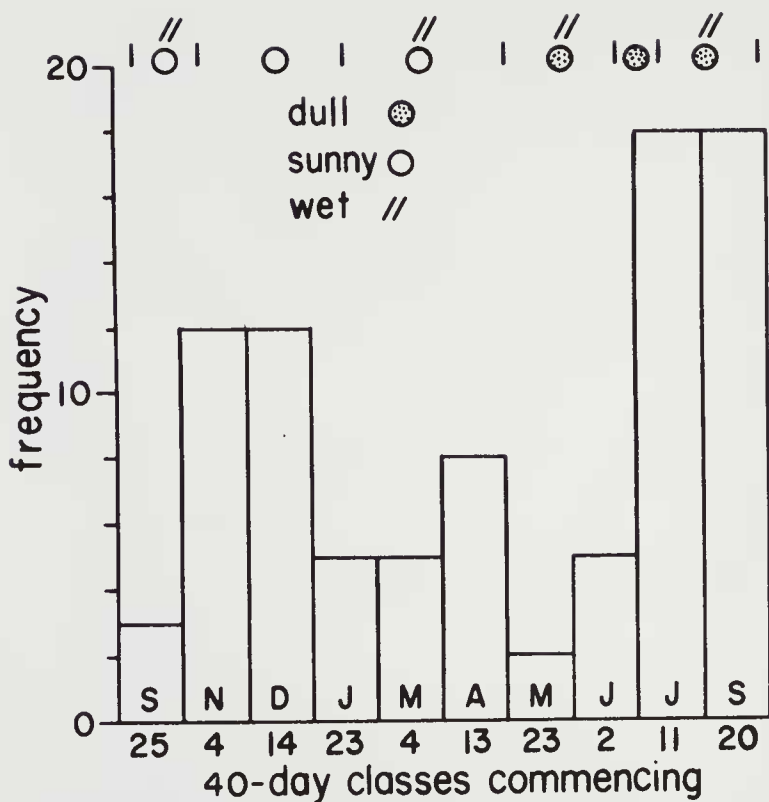


Fig. 5. Totals of *Anomma nigricans* trapped, in 40-day classes; with the seasons in the nearby forest zone indicated.

was caught after the trapping of a far greater number of individuals than extrapolation would have predicted: 3685 as against c. 180.

Table I gives the monthly rainfall and mean daily hours of bright sunshine per month for the period under review: by bright sunshine is meant sunshine as measured by a Campbell-Stokes' or similar apparatus. The rainfall and monthly totals of *Alaopone atriceps* were compared, using Spearman's rank correlation:

$$n = 13$$

$$R = 317$$

$$p = > 0.1$$

This confirmed what is suggested by inspection: rainfall and numbers of male dorylines are neither directly nor inversely associated, nor can a lagged correlation be detected.

However, there is a highly significant deviation from a random distribution pattern in the three components of Table 1 (extension of the median test (Siegel 1956): $\chi^2 = 16.15$, $DF = 3$, $p < 0.001$). There is in fact an association of peak numbers, both in *A. atriceps* and overall ant frequencies (Fig. 3), with the period of the year—late April through early June (Fig. 1)—when both mean sunshine and mean rainfall are relatively high. This is obscured in the data of Table 1 by October 1969 and January and February 1970 being wetter than usual.

DISCUSSION

Cyclic phenomena occur in all the New World dorylines studied (Schneirla, 1971, and works cited therein): brood production and a division of activity between well marked statary and nomadic phases are among the events in which regular periodicities are the

Table 1. Bright sunshine, rainfall and numbers trapped of *Alaopone atriceps*, corrected for missing samples and grouped in monthly classes.

	Mean bright sunshine/hrs per day	Rainfall cms	<i>A. atriceps</i> trapped
1969			
Oct	7.9	10.21	34
Nov	8.7	1.12	29
Dec	8.9	0.64	106
1970			
Jan	8.0	7.54	38
Feb	8.1	8.33	57
Mar	8.3	3.76	178
Apr	6.5	6.71	624
May	6.3	25.78	707
Jun	6.3	15.80	237
Jul	5.2	2.49	124
Aug	4.9	0.76	191
Sep	6.5	3.76	104
Oct	7.7	8.46	41

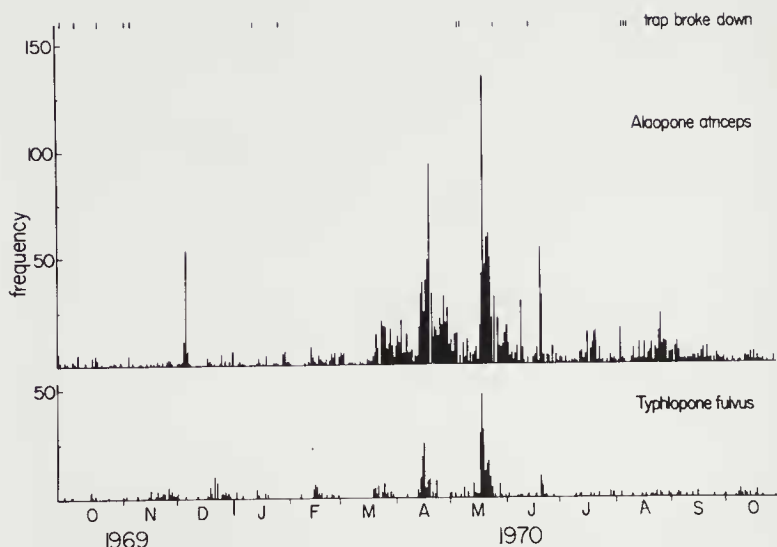


Fig. 6. Daily frequencies of the two most abundant species in the Legon trap samples, with days of missing samples indicated.

rule. However, in the Old World Dorylini examined—mainly in *Anomma*—Raignier and van Boven (1955) denied such cyclic behaviour to be present. My data (Figs. 3, 4) suggest 1) males are produced, at least by the five most common species, throughout the year, 2) there is a regular annual cycle in the timing of male flights, 3) this cycle is synchronous in the four most abundant species (and perhaps in all), 4) males are emitted about every 30 to 32 days between about March through September—around every 28 or 29 days in December through February.

Just as Rettenmeyer (1963) was able to confirm the presence of Schneirla cycles in a wide range of Neotropical and Nearctic Ecitonini species the present figures indicate that such cycles hold true in the Ethiopian Dorylini—and presumably too the Oriental, for they are for the most part congeners. But Raignier and van Boven were correct in noting the production of males throughout the year, confirmed by Haddow *et al.* (1966) through light-trap sampling. The phenomenon is still undetected in Ecitonini. Neither the observations of Rettenmeyer (1963) nor of Kannowski (1969) were conducted during a complete calendar year but the temporal spread of the latter's positive scoring of, for example, alate males of *Labidus*

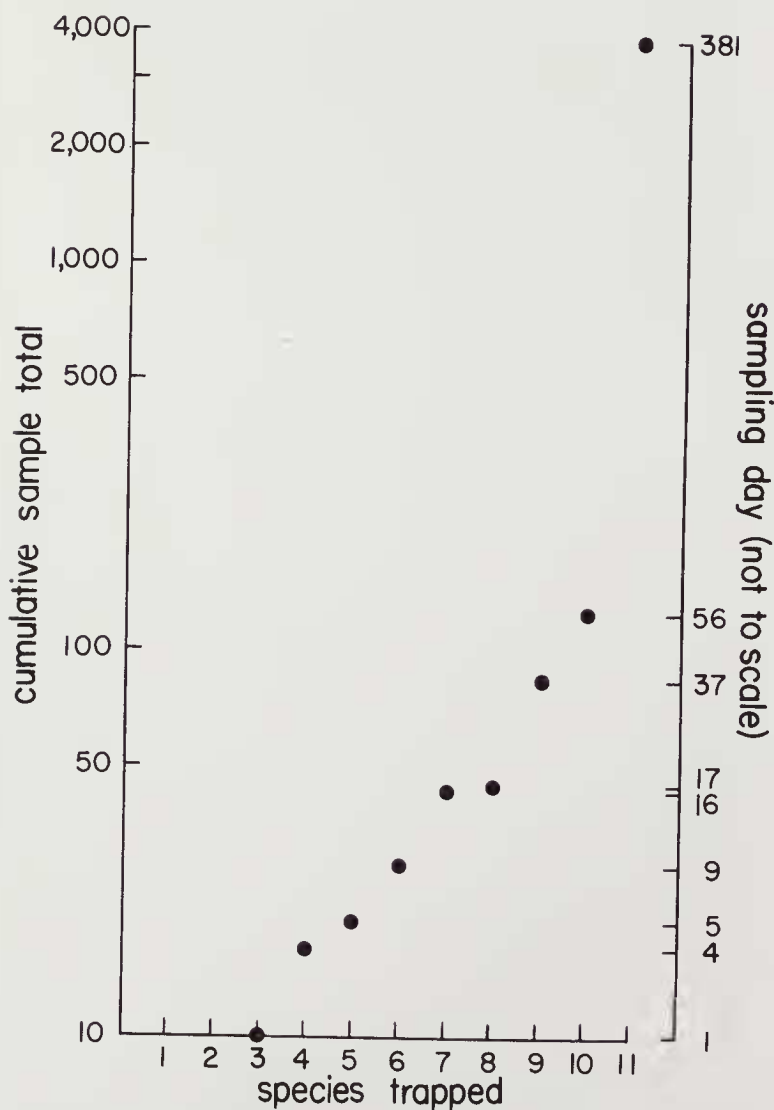


Fig. 7. Arrival days (not to scale), cumulative sample size (logarithmic) and the cumulative species trapped.

praedator (F. Smith)—March 7 to May 30—is suggestive either of the production of more than one sexual brood by the colonies or that each colony is out of step with its conspecifics.

An alternative interpretation of my figures is possible: each colony of a species could be out of phase with its neighbours, in which case each burst of alate males trapped would have come from a distinct colony. Field observations, however, suggest colonies of the surface foraging species—*Typhlopone fulvus* and *Anomma nigricans*—are too widely dispersed to support this hypothesis.

Except for *Anomma nigricans*, the common black driver ant of the forest zone (Haddow *et al.*, 1966), the species concerned are believed to be predominantly non-nomadic—even, it seems, *Typhlopone fulvus*, the common brown driver ant of the forest area (Wheeler 1922). There is no positive evidence at present for the cyclic emission of males to be associated with migratory periodicities, except in *Anomma* species (Raignier and van Boven, 1955).

That the period between peaks in April, May and June (Fig. 5) is longer than in December and January is to be expected: the months December through February are the hottest ones. But are these cycles of about 30 days in the emission of alate males the concomitant of an egg-to-egg cycle in worker brood production?

In their study of *Anomma* Raignier and van Boven (1955) note the period from 1st instar larva to alate adult males to occupy 40 to 52 days, to be followed by a preflight stage of 10 days. They give no information on the duration of the egg stage and their account is somewhat obscured by a confusing larval nomenclature, but they conclude broods of males take twice as long to develop as broods of females and that a colony with male brood remains at one place for twice as long as the normal. This confirms my view that Raignier and van Boven are wrong in denying the existence of cycles in *Anomma*. The data can be interpreted as showing a 30-days cycle to be present, male production occupying two consecutive cycles. That a colony may produce multiple out-of-phase broods is not excluded by this theory.

Comparing the flights of alate male *Anomma* with those of other, non-doryline, species, Raignier and van Boven state of the former '... ces vols ne sont pas des vols nuptiaux mais uniquement des vols de dispersion.' Unless 'dispersion' here means something other than migration or spreading it is impossible to follow this. The only adaptive significance one can accept is the reverse of what these

authors propound: the flights of male dorylines have a genetic role, one that is doubly important in view of the limited dispersal attributes of the flightless females.

The conclusion of Haddow *et al.* (1966), that 'seasonal fluctuations . . . are probably not much greater than the night-to-night variations . . .' is unsupported and results from the defects in their sampling method, noted below. Figs. 3 and 4, to a lesser extent Fig. 5, demonstrate a marked seasonal periodicity in frequencies.

The peak emission of males by Dorylini at Legon during the first wet sunny season of Gibbs and Leston (1970) is concurrent with the production of maximum numbers of alates in the ubiquitous and arboreal-nesting formicine *Oecophylla longinoda* (Latreille) (Leston and Gibbs, 1971) and in the similar nesting but strictly forest-zone myrmicine *Macromischoides aculeatus* (Mayr) (Aryeetey, 1971). The peak in *Anomma* approximates that found in the ground-nesting forest ponerine *Odontomachus troglodytes* Santschi (Gibbs and Leston, 1970); during the second wet sunny season, a season not clearly delimited at Legon but distinct in the nearby forest zone (Fig. 5).

In *Oecophylla* and *Macromischoides* it appears that the ultimate factor is the optimization of conditions for the production of the first broods by the solitary queen (Leston, 1972). After the end of the first wet sunny season there is a dramatic drop in the available prey (Gibbs and Leston, 1970) and a reduction too in mean temperature. However, colonies are not, in Dorylini, founded by a single, claustral queen but by budding. It is suggested the ultimate factor in the production of sexuals in Dorylini is the availability to the parent colony during the beginning of the first wet sunny season, of abundant insects and earthworms, their known prey (Gotwald, 1974).

The annual peak (Fig. 3) falls within the wet sunny period, April through to the end of May (Fig. 1). In the nearby forest zone this wet sunny season is longer and there is, too, a second one later in the year (Fig. 5).

The attempt to fit all biological periodicities in the humid tropics into an alternation of wet and dry 'seasons' still persists. Thus Karr (1976): 'Life history adaptations to seasonal changes in rainfall are well documented.' Karr then lists no fewer than 22 papers in support—including Gibbs and Leston (1970), which says just the reverse! Kanno's (1969) conclusion—'The interface between the wet and dry seasons appears to be the most important time of the

year for army ant nuptial flight activity in the region of Barro Colorado Island'—is in accord with my data, and indicative of this interface being in fact a wet sunny period.

The fauna of Legon is a complex mix of forest relicts, secondary successional species and true savanna forms: investigations have covered such diverse groups as snakes, ponerine ants, hemipters and mantises (Leston, 1972, 1979). In practice it is seldom difficult to categorize a particular animal by habitat. The relative numbers, in a degraded forest habitat, is a function of the degree of deforestation—most species are not directly climate-limited—modified by the varying abilities of savanna taxa to saltate (Leston, 1979).

The traps reported on by Haddow *et al.* (1966) covered both tropical forest and degraded forest but unfortunately the results are given in pooled form, making a numerical habitat comparison difficult: the pooling of data from three traps run at different times of the year makes an investigation of periodicities equally impossible. But overall, despite species differences—which probably reflect an oversplitting taxonomy—there is a marked similarity in the dorylines trapped at Legon, on the edge of the Guinea forest bloc, and that of Entebbe, 3,600 km distant on the edge of the Congo forest bloc.

As at Legon, the most abundant species at Entebbe was an *Alaopone*: these are hypogeic ants of degraded forest habitats. *Typhlopone fulvus*, assumed by Haddow *et al.* (1966) and Wheeler (1922) to be hypogeic, was also numerous at both localities: my field observations show it frequently forages at the surface in forest and degraded forest areas. Some *Dorylus sensu stricto* were frequent at both sampled places: probably for the most part savanna ants which invade degraded forest. *Anomma* species were relatively infrequent at both too: as noted above they are essentially genuine forest dwellers, surface foraging, the 'notorious driver ant' (to cite Haddow *et al.*). *Rhogmus fimbriatus*, about as frequent at Entebbe as at Legon, is a hypogeic, mainly savanna, species.

The similarity of the two faunas over an extensive transcontinental area suggests a widespread pattern of resource partitioning but why the alates should space themselves out in male flights through the hours from dusk to dawn, as Haddow and his colleagues indicate—found too in the American Ecitonini (Kannowski, 1969)—is less easy to interpret in such terms. And the most remarkable feature of the Legon results, the synchrony of the species' cycles,

remains to be placed in an evolutionary context. I cannot accept that synchrony results from a climatic shock bringing the species annually into phase: these are social insects, as adept as other ants in modifying their environment (Leston, 1973), whilst weather-induced synchrony is likely at best to extend over a few weeks only, not over a 400 day period as noted here.

That all Old World dorylines studied—including Aenictini—have nocturnal male flights is indicative primarily, I believe, of high humidity preferenda: after all, these are hypogeic or, at least, ground-nesting species. The diel spacing out of flight times is consistent with this: relative humidity in the wet tropics is minimal around 1500 hrs local time, maximal around 0500 hrs. The immediate post-dusk species are less tied to the highest RH value than are the pre-dawn ones. The species' synchrony, I suggest, has evolved as a mechanism for oversaturation by potential prey. Male dorylines have large flight muscles—protein—and much fat: they are preyed upon by frogs and toads (Wheeler, 1922) and probably a wide range of other nocturnal predators whilst isolated males, once landed, fall victims of the ever-present dominant ants.

The logarithmic relationship in the species' frequencies (Fig. 2) follows the pattern noted for many animals by Williams (1964) and others. It is paralleled in several organisms sampled in Ghana: mist-netted lower-storey birds, field collected snakes, pyrethrum knock-downed non-doryline ants and ultraviolet light-trapped paussid beetles, amongst others (Leston, 1972).

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CONCLUSIONS

1. In an ultraviolet light-trap run for 400 days at Legon, Ghana, males of eleven species of doryline ants, in *Dorylini*, were captured.

2. The relative frequencies approximated a logarithmic sequence.
3. The annual peak occurred in the first wet sunny season.
4. Additional to the annual cycle peaks occurred about every 30 days.
5. The more frequent species showed fluctuations in parallel.
6. It is suggested Schneirla cycles were present in the species sampled.
7. The ultimate factor in the annual production pattern is probably the availability of food to the parent colony.

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